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Cephalopod Predation Facilitated by Dinoflagellate Luminescence

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Abstract. Predation by nocturnal cephalopods on nonluminous prey was examined in the presence of dinoflagellate bioluminescence. *Sepia officinalis* Linnaeus and *Euprymna scolopes* Berry were tested for predation efficiency in darkness illuminated by the luminescent dinoflagellate *Pyrocystis fusiformis* Murry. Prey were mysids, *Holmesimysis sculpta* (Tattersall); grass shrimp, *Palaemonetes pugio* Holthuis; and mosquito fish, *Gambusia affinis* Baird and Girard. Tests were conducted in aquaria containing 0–20 cells ml^{-1} of *P. fusiformis*. Predation increased as numbers of luminescent dinoflagellates increased. Controls were predation tests in the presence of *P. fusiformis* during nonluminescent photophase or in the absence of dinoflagellates. Movements of squid and prey readily stimulated luminescence. Behavior and correlated luminescence in infrared-illuminated aquaria were recorded by image-intensified and infrared video cameras. *Sepia* strikes on prey were common under luminescent conditions—85% occurred in less than 10 min; but strikes in darkness were rare. *E. scolopes* attacked more frequently than *Sepia*, and almost 90% obtained prey under luminescent conditions. This study demonstrates the ability of squid to use dinoflagellate bioluminescence to locate and capture nonluminous prey. The burglar alarm theory of the adaptive significance of dinoflagellate bioluminescence is supported.

Introduction

At least 20 functions of bioluminescence have been advanced (Tett and Kelly, 1973; Buck, 1978). One of these, the burglar alarm theory, holds that light produced by luminescent prey upon attack by a predator might attract its own predators, thereby reducing predation pressure on the bioluminescent organism. The result would be of little use to the prey unless it survived the attack, for which there is some experimental evidence in dinoflagellates (Buskey *et al.*, 1985). However, even with prey mortality, benefit could accrue to the species as a whole by such a process. This is particularly true in dinoflagellates, which tend to exist in localized clones, so that the sacrifice of some members of the clone would directly favor survival of the luminescent genotype (Burkenroad, 1943). The theory is supported by demonstration that organisms apt to graze on luminescent dinoflagellates are induced by luminescence to undertake evasive behavior that would tend to reduce grazing (Esaias and Curl, 1972; White, 1979; Buskey and Swift, 1983). Until recently, however, there has been little evidence for the second critical element of the theory, namely that higher level predators are able to hunt animals efficiently by the light these latter trigger from bioluminescent organisms, either by feeding on or by moving among them.

Mensinger and Case (1992) showed that juvenile midshipman fish, *Porichthys notatus* Girard, midwater ambush predators, feed efficiently on nonluminescent prey by dinoflagellate light. Here we extend these observations to the Cephalopoda, predators with superb vision (Young, 1991) and remarkably developed hunting behavior. Demonstration that these invertebrate predators are able to hunt effectively with the aid of bioluminescence strongly reinforces the burglar alarm theory. The work also has implications for interpretation of the role of luminescence in the population dynamics of marine organisms.

As predators we used *Euprymna scolopes* Berry, a shallow benthic squid indigenous to the Hawaiian archipelago (Singley, 1983), and *Sepia officinalis* Linnaeus, a benthic-to-midwater cuttlefish found in the Eastern Atlantic Ocean

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and the Mediterranean Sea (Boletzky, 1983). *E. scolopes* tends to approximate the ambush attack of the midshipman fish, but from a position on the bottom. *S. officinalis* differs markedly from the midshipman fish in hunting behavior by roving actively in the midwaters.

E. scolopes adults eat primarily mysid shrimp; in aquaria, the young also take *Artemia* (Singley, 1983). Members of this species are active only at night, when they are able to produce bioluminescence from a light organ populated by luminescent bacteria (Singley, 1983; McFall-Ngai and Montgomery, 1990). They camouflage themselves in the sand during daylight. A feeding strategy consisting of approach, tracking, and capture phases, similar to that of *Sepia*, has been reported in other squid (Foyle and O'Dor, 1988). However, our laboratory observations show that *E. scolopes* actually tends to wait for the approach of prey.

S. officinalis adults are roving nocturnal predators that feed on a variety of prey including small crustaceans, fish, or even smaller *Sepia* (Boletzky, 1983). The young eat mainly small crustaceans. The day is spent in the sand and they rise into the water column at night to hunt, aided by a diurnal cycle of buoyancy change (Denton and Gilpin-Brown, 1961). Their vision is excellent and they use both binocular and monocular fixation to locate prey (Messenger, 1968). Attack is by one of two strategies, depending on prey size and potential risk to the attacker: (1) rapid extension of the two prehensile tentacles, or (2) envelopment of the prey (Duval *et al.*, 1984). The tentacle extension process has three phases—attention, positioning, and seizure. The first two are visually controlled, whereas the last is so rapid that there is no time for visual feedback. Accuracy consequently depends on reducing the visual error to near zero (Messenger, 1968).

Materials and Methods

Collection and maintenance of experimental animals

Juvenile and adult *Euprymna scolopes* were generously provided by Professor M. McFall-Ngai, who periodically collected specimens from Kaneohe and Niu Bays on the coast of Oahu, Hawaii. Animals were kept in a 40-gallon aquarium with single-pass, heated seawater (20° −24°C) and a 1.0-cm-deep sand bottom. Experimental animals were kept on a 12:12 light-dark (LD) cycle, the same LD cycle as the rest of the animals in this study. Food consisted of brackish-water grass shrimp (*Palaemonetes pugio* Holthuis). All experiments reported here were done with adults.

Juvenile cuttlefish, *Sepia officinalis*, were purchased from the University of Texas Marine Biomedical Institute, Galveston, Texas (Boletzky and Hanlon, 1983; DeRusha *et al.*, 1989). They were kept in 60-gallon aquaria with single-pass seawater (14° −18°C) and 2.5-to-3.8-cm-deep sand bottoms. All animals in this study were maintained on the same 12:12 LD cycle. Mortality was low, with good survival to reproductive age. Animals used in these experiments were about 2 months old and averaged 25 mm in length. Food consisted of kelp-canopy mysids (*Holmesimysis sculpta* [Tattersall]); top smelt (*Atherinops affinis* Aries), both live and frozen); striped shore crabs (*Pachygrapsus crassipes* Randall); and mosquito fish (*Gambusia affinis* Baird and Girard). Prey varied according to cuttlefish size and food requirements.

The various food and prey animals were obtained and handled as follows. Mysids were collected weekly by dip netting from kelp canopies along the Santa Barbara coast; maintained in aerated, free-flowing aquaria; and used within 10 days of capture. Mosquito fish were obtained every 2 weeks from a local aquarium store; fed daily; and maintained in a 50-gallon aerated, fresh-water tank. Grass shrimp were obtained periodically from a local supplier; maintained in brackish water at room temperature; fed weekly; and used within 15 days. All prey animals appeared to remain in excellent condition during the specified holding periods.

Dinoflagellate culture and luminescence cycle

Unialgal cultures of the dinoflagellate *Pyrocystis fusiformis* Murry were originally supplied by the late B. M. Sweeney and maintained using the techniques of Widder and Case (1982). Cells were maintained on the same 12:12 LD cycle as the squid at between 18° and 20°C, in sterilized filtered seawater enriched with f/2 formula (Guillard and Ryther, 1962) and soil extract, omitting silicate. During the day-phase, cells were illuminated from above with cool-white fluorescent bulbs at 500 μW cm^{-2} as measured by a United Detector Technology Model 40× photometer. Two populations were maintained on opposite LD cycles for simultaneous use of day- and night-phase cells. On experimental days, cell concentrations were determined with a cell-counting chamber (Hausser). Under these conditions, maximum scotophase bioluminescence intensity was 10^{10} photons · cell^{-1} s^{-1}.

Optimal controls for this study would involve use of completely nonluminescent photophase dinoflagellates. However, although the cells used in control experiments were at least 3 h into photophase, as soon as they were placed in darkness at the beginning of the experiment they rapidly recovered enough luminescent capacity to aid vision of the squid. To assess the magnitude of recovery as a function of time in the dark, tests were conducted to quantify mechanically excitable bioluminescence. Cells used for this test were at least 5 h into scotophase. Quantum emission was measured in a 10-in-diameter integrating sphere collector (Labsphere, Inc.), with an RCA model 8850 photon-counting photomultiplier operating

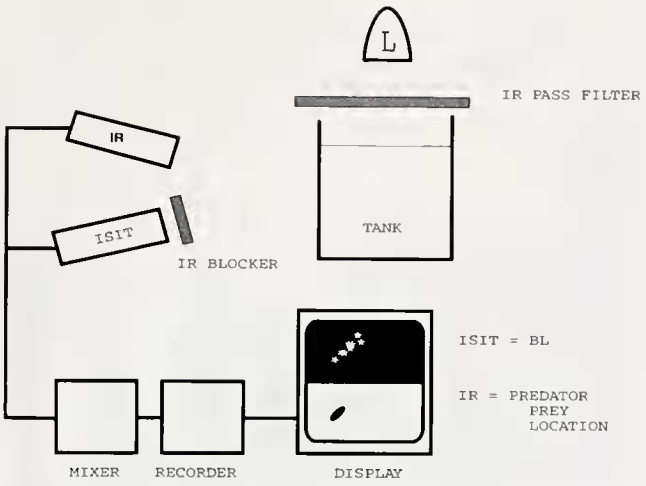

Figure 1. Split-screen video camera arrangement for monitoring predator/prey interactions.

at −1680 V (Latz *et al.*, 1987). Cell samples were stimulated to exhaustion with a stirring rod consisting of a stainless steel shaft with three cross tines, coupled to a DC motor (Latz *et al.*, 1990) operating at a standard speed. Motor speed was measured with a magnetic pick-up mounted on the motor shaft and displayed on a Visi-tach digital ratemeter. Light emission was monitored for 250 ms by ACE-MCS software operating with a channel dwell time of 5 ms. Previously unstimulated cells were run every 15 min for 3 h.

Quantitative predation experiments with Sepia officinalis

Twelve tests with single animals in 12-liter glass tanks were run concurrently in a darkroom. Six were controls, either with dinoflagellates absent or in photophase; and six were experimental tanks with dinoflagellates in scotophase. Tanks were separated by opaque dividers. Water temperature was maintained at 15°C. *S. officinalis* (average mantle length = 23.3 mm ± 0.39; n = 50) were placed in individual tanks no later than 1 h before onset of the dark cycle to allow recovery after transfer. Dinoflagellates in final concentrations of 1, 2, 5, 10, 15, and 20 cells/ml were added 2 h after onset of scotophase. Because cells tend to settle over time, concentrations indicated are for initial conditions. With care taken to minimize bioluminescence, 10 mysids (carapace length: 1.9 mm to 3.6 mm) were added simultaneously to all tanks. Preliminary experiments of up to 6 h were conducted to determine optimal time span and prey density. Results showed that *Sepia* of the ages used (2 to 4 months) were satiated after 3 h and never consumed more than 10 mysids during that time. To minimize disturbance and maintain dark adaptation, the *Sepia* were handled with the aid of an IR-light and IR-image converter. At the end of an experiment, the surviving mysids were counted after the cephalopods had been returned to their home tanks. Experimental tanks were emptied and the sand was washed free of dinoflagellates every night and refilled with filtered seawater the next morning. The laboratory filtering system ensured that the seawater was free of other visibly bioluminescent organisms.

Predator/prey interactions

Behavior of *S. officinalis* and *E. scolopes* was monitored with DAGE MTI image-intensified (ISIT-66LX) and infrared (IR) (SC-66LX) video cameras during predator/prey interactions. The aquarium was illuminated from above by a 25-W incandescent lamp screened by a Kodak IR filter (Wratten No. 87), eliminating wavelengths shorter than 700 nm. A Panasonic special-effects generator (WJ-4600A) produced a horizontal split-screen image of the aquarium. Half of the screen displayed the animals as viewed under IR light, and the other half displayed dinoflagellate luminescence as viewed by the ISIT. The ISIT was fitted with a red-absorbing blue-green glass filter (Melles-Griot BG 18) to block wavelengths longer than 650 nm. Data were stored on a Sony Hi-8 EV C100 video recorder and transferred to a Power Macintosh 8100/80 AV computer for detailed analysis. The experimental arrangements are shown in Figure 1.

In work with *S. officinalis*, 2 h after onset of the dinoflagellate scotophase a single cuttlefish was placed in a 10-l aquarium containing 40 cells ml^{-1} of dinoflagellates. Tank size was determined by limitations of camera resolution. A single mosquito fish (length = 23–36.4 mm)

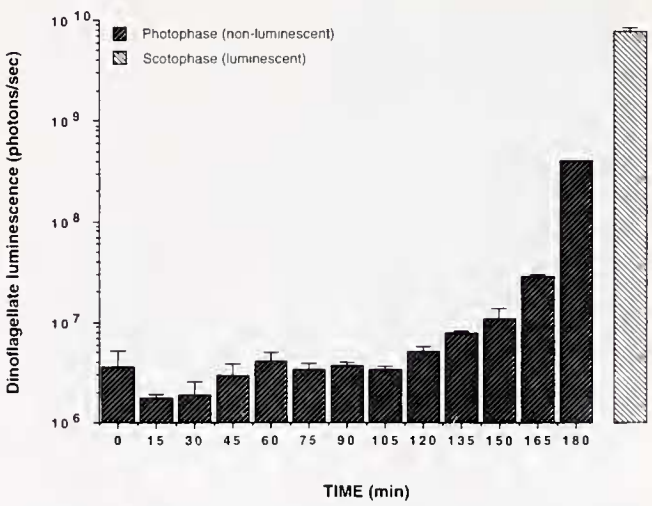

Figure 2. Luminescence produced by photophase dinoflagellates (*Pyrocystis fusiformis*) over a 3-h period after transfer to darkness as compared with cells in scotophase. Error bars represent standard errors.

was added 15 min later. Optimal prey size was determined by the aggressiveness of *Sepia*, which ignored small targets. Events were monitored for a subsequent 30 min with the ISIT/IR video recording system. Four trials were conducted on a given day, for a total number of 20 runs over a 2-month period.

With *E. scolopes*, procedures differed slightly owing to its smaller size. An hour prior to the night cycle, each test animal (average mantle length = 14.15 ± .34 mm; $n = 10$) was moved to an individual 3.5-l experimental aquarium and allowed to acclimate for 3 h. Tank size was small to ensure that strikes could be recorded with high resolution. Each tank was aerated and kept at the same temperature as the holding aquarium (~23°C). Dinoflagellates in final concentrations of 0, 5, 10, 20, and 40 cells/ml were added slowly from a wide-mouth container into each tank to minimize premature stimulation. A single grass shrimp (carapace length = 8.2—11.7 mm) was added 15 min after the dinoflagellates to allow calming time for the squid. *E. scolopes* are significantly harder to feed in captivity than *Sepia*. The prey chosen for this experiment was both familiar to them and large enough to attract their attention. Monitoring continued for a subsequent 30 min. Trials ($n = 5$) were conducted daily, for a total of 90 runs over a 3-month period. Interactions of predators and prey were monitored and analyzed with the same split-screen apparatus used for *Sepia* (Fig. 1).

Results

Dinoflagellate luminescence recovery upon light to dark transfer

P. fusiformis in photophase proved difficult to use as a control because cells became luminescent relatively quickly after being placed in the dark. A similar phenomenon has been observed in *Pyrodinium bahamense* (Biggley *et al.*, 1969) and *Pyrocystis lunula* (Colepicolo, 1992). Our results showed increasing luminescence with passage of time in darkness (Fig. 2). After 3 h in darkness the light produced by 20 cells/ml of photophase *P. fusiformis* is comparable to that produced by 1 cell/ml in full scotophase (Fig. 2). This intensity is sufficient to improve the feeding accuracy of *Sepia*. Therefore, to ensure complete darkness, subsequent controls in our experiments contained no dinoflagellates. This would appear reasonable because no adverse effects on the squid or prey were ever seen for the concentrations used; mortality was quite low for both species of cephalopods over the 19-month experimental period.

Predation experiments

These experiments were conducted exclusively on *S. officinalis*. After an acclimation time of 3 h, all animals were behaving normally, hovering above the sand and feeding. Tanks containing *P. fusiformis*, both scotophase (test) and photophase (control), had fewer mysids present at the end of the experiment than did tanks without dinoflagellates. In control tanks containing photophase dinoflagellates, the average number of mysids consumed was from 0.88 to 4.75, increasing with dinoflagellate concentration (Student's *t*-test; no significant difference at any concentration, $P > 0.078 - 0.662$; Fig. 3). This effect is attributed to recovery of luminescent capacity in the course of the experiment. Confirmation comes from the fact that the average number of mysids consumed in tanks containing no dinoflagellates was 0.2 (Fig. 4). By contrast, in the tanks containing scotophase, fully luminescent dinoflagellates, the number eaten varied from 4.2 to 8.0, increasing with dinoflagellate concentration (ANOVA and Dunnett one-sided test; $P < 0.015$; Fig. 4). Thus predation of cuttlefish on mysids was correlated with the presence of scotophase dinoflagellates (*Pyrocystis fusiformis*). Unlike the situation reported for the midshipman fish, *Porichthys notatus* (Mensinger and Case, 1992), no significant inhibition of predation was observed at high dinoflagellate concentrations.

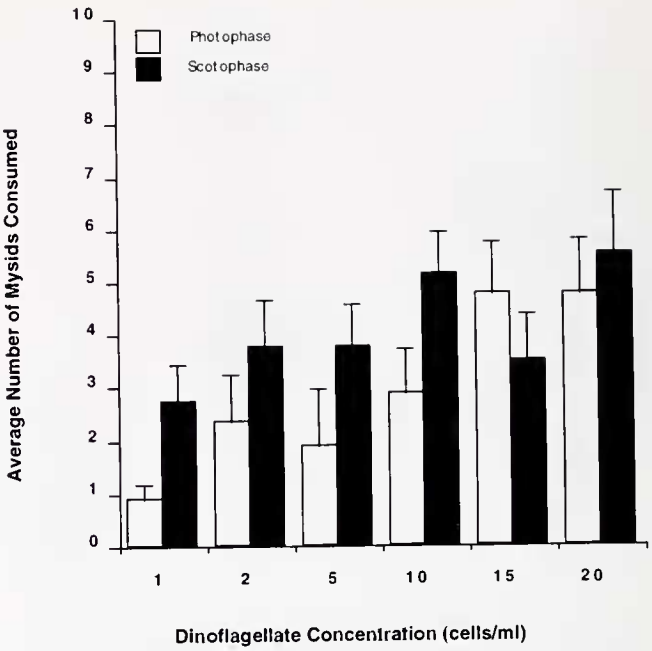

Figure 3. Average number of mysids (*Holmesimysis costata*) consumed by cuttlefish (*Sepia officinalis*) as a function of concentration of scotophase and photophase dinoflagellates (*Pyrocystis fusiformis*). Photophase cells become luminescent as time in darkness progresses (see text). Error bars represent standard errors.

Observations of predator-prey interactions

The dual camera system allowed simultaneous viewing of predator-prey interactions and the resultant lumines-

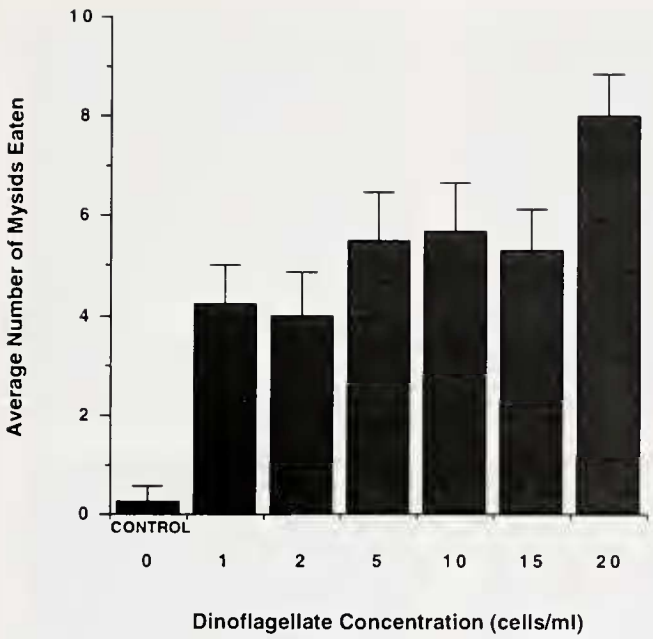

Figure 4. Average number of mysids (*Holmesimysis costata*) consumed by cuttlefish (*Sepia officinalis*) as a function of concentration of luminescent dinoflagellates (*Pyrocystis fusiformis*). Error bars represent standard errors.

cence. No behavioral change was noted between organisms in holding or experimental tanks; thus it was assumed that any direct effect of dinoflagellates (exclusive of bioluminescence) at all concentrations was insufficient to bias the experiments. In experimental runs the dinoflagellate concentration was 40 cells ml^{-1}. Controls for this experiment were conducted without dinoflagellates.

Strikes by *Sepia* and *E. scolopes* were easily discernible using both the IR and ISIT camera (Figs. 5 and 6). Details as fine as eye movements tracking the luminescence were visible with the IR camera. Mosquito fish were observed to trigger luminescence with each tail stroke, which *Sepia* monitored closely. Grass shrimp appendages triggered ample luminescence to attract the attention of *E. scolopes*.

Cuttlefish strikes were all or none, and misses were never observed in a total of 20 attacks. A strike or other rapid movement elicited a large cloud of luminescence that was easily observed with the ISIT camera, but the normal rise and hover movements of *Sepia* triggered no luminescence. Due to acclimation time (15 min), *Sepia* feeding behavior was not affected by the confines of the aquaria, and strikes were primarily away from aquarium walls. Mosquito fish appeared to swim normally under the experimental conditions. Sixty-five percent of the *Sepia* in the presence of scotophase dinoflagellates were successful in prey capture, whereas only 5% of the animals in the control tank (no luminescence) obtained prey (Chi-square test; $P < 0.0001$). Eleven individuals in the presence of luminescence took less than 10 min to capture prey, and all strikes occurred in under 20 min. In the control tanks, only one strike occurred out of 20 tests, and this occurred after almost 30 min (Fig. 7).

Messenger (1968) defined the attack of *S. officinalis* as including three components: attention, positioning, and seizure. Attention, the interval between the time when the prey enters the field of view and when the cuttlefish and prey are on the same axis, can take less than 1 s or it may last for up to 10 s (Messenger, 1968). In this study, the average duration of attention was 10.9 s (SE = ±2; n = 10). Positioning, which begins when the cuttlefish faces the prey and ends with the strike, can last from less than 1 to more than 10 s (Messenger, 1968). During our experiments, *Sepia* averaged 7.3 s (SE = ±1.1; n = 10) for this component of the attack sequence. The final act, seizure, is marked by the extension of the tentacles and ends with the prey held by all arms, taking about 2 s (Messenger, 1968). Our specimens accomplished this in an average of 0.83 s (SE = ±0.05; n = 10).

E. scolopes has a different attack mode. Instead of the hover and strike method of the cuttlefish, *E. scolopes* remains poised on the bottom, frequently in a depression deliberately made by blowing sand with the siphon, where it waits for prey to move within its strike zone. The size of the strike zone varies with each animal but is typically a circle, with the squid at its center, whose radius is about twice the body length of the animal. Once a target is in that strike zone, the squid rapidly turns, points all arms in the direction of the prey, and strikes by launching its two tentacles, as with *Sepia*. Our video analysis shows no evidence, by body movement or other sign, of the attention component noted in the cuttlefish. The actions of *E. scolopes* are similar to those of an ambush predator, going from sedentary directly and rapidly to positioning and seizure. Unlike *Sepia*, *E. scolopes* does not adjust its distance to the prey during positioning. Were it not for the launching of the tentacles, positioning and seizure by this squid would be considered one step. The average time taken by *E. scolopes* for positioning was 1.1 s (SE = ±0.09; n = 10) and for seizure, 0.63 s (SE = ±0.03; n = 10). When a miss occurred, the squid did not pursue the prey and continue the attack immediately, even though the prey's luminescent track was distinct. All movement was easily discernible on the monitor with the ISIT camera, including luminescence induced by siphon exhaust as the squid excavated a resting place in the sand. Motion by the grass shrimp prey, both "walking" along the bottom and swimming, stimulated dinoflagellate luminescence. No noticeable attention was given to prey outside the strike zone.

There was a significant increase in frequency of predation in aquaria containing luminescent dinoflagellates (Fig. 8). In the absence of luminescence, *E. scolopes* struck

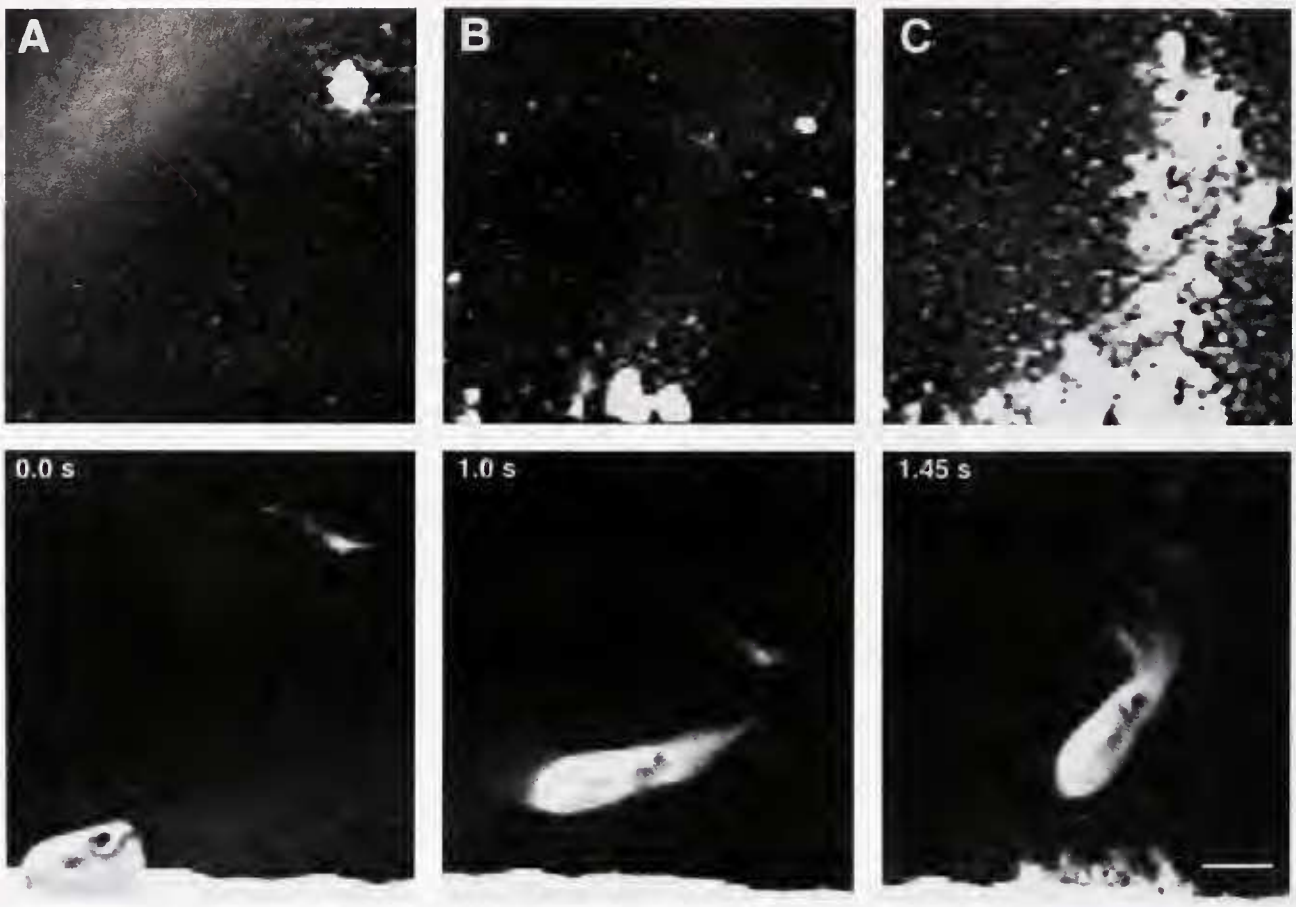

Figure 5. Split-screen video image of *Sepia officinalis* feeding on ghost shrimp (*Palaemonetes pugio*). Image-intensifying camera, top view. Infrared camera, bottom view. (A) Attention; (B) Positioning; (C) Seizure. Luminescence is produced by *Pyrocystis fusiformis* upon being stimulated by ghost shrimp movements. Bar scale = 2 cm.

in only 37% of the total tests (Chi-square test; $P < 0.008$). Under luminescent conditions the frequency was higher: 79% with 20 cells/ml and 63% at a concentration of 40 cells/ml. Comparisons made between concentrations showed no significant differences (Chi-square test; $P = 0.76$), nor did a comparison of strike *rate* among all concentrations (ANOVA and Dunnett one-sided test: $P = 0.46$).

Discussion

Cephalopods employ many sophisticated sensory organs during prey capture, namely eyes, statocysts (Budelmann, 1979), and lateral line analog (Budelmann *et al.*, 1991). Stimuli that induce attacks appear to be primarily visual since prey in an adjacent aquarium are just as likely to be attacked as those swimming in the same aquarium with the cephalopods (Wells, 1958). Both *S. officinalis* and *E. scolopes* are nocturnal predators living in waters where bioluminescent dinoflagellates are present in notable quantities: 11 dinoflagellate cells l^{-1} in the Northeastern Atlantic and >1 cell l^{-1} for tropical waters, to a depth up to 150 m or more depending on clarity and mixing (D. Lapota, pers. comm.). Dinoflagellate concentrations used in these experiments exceed those that occur naturally but are lower than concentrations used in previous burglar alarm studies (Esaias and Curl, 1972; White, 1979; Buskey *et al.*, 1983). Some of the lower concentrations used in our study are not unusual in dinoflagellate bloom conditions.

Locomotion of mysid (*Holmesimysis sculpta*), mosquito fish (*Gambusia affinis*), and grass shrimp (*Palaemonetes pugio*) readily stimulated dinoflagellate (*Pyrocystis fusiformis*) luminescence at all concentrations, illuminating the prey and thereby increasing their susceptibility to squid predation. Their swimming hydrodynamic forces approximate the 1.0 dyne cm^{-2} required to excite luminescence by couette flow (Latz *et al.*, 1994). Luminescence appeared to be the primary factor in inducing predation, as the absence of dinoflagellates resulted

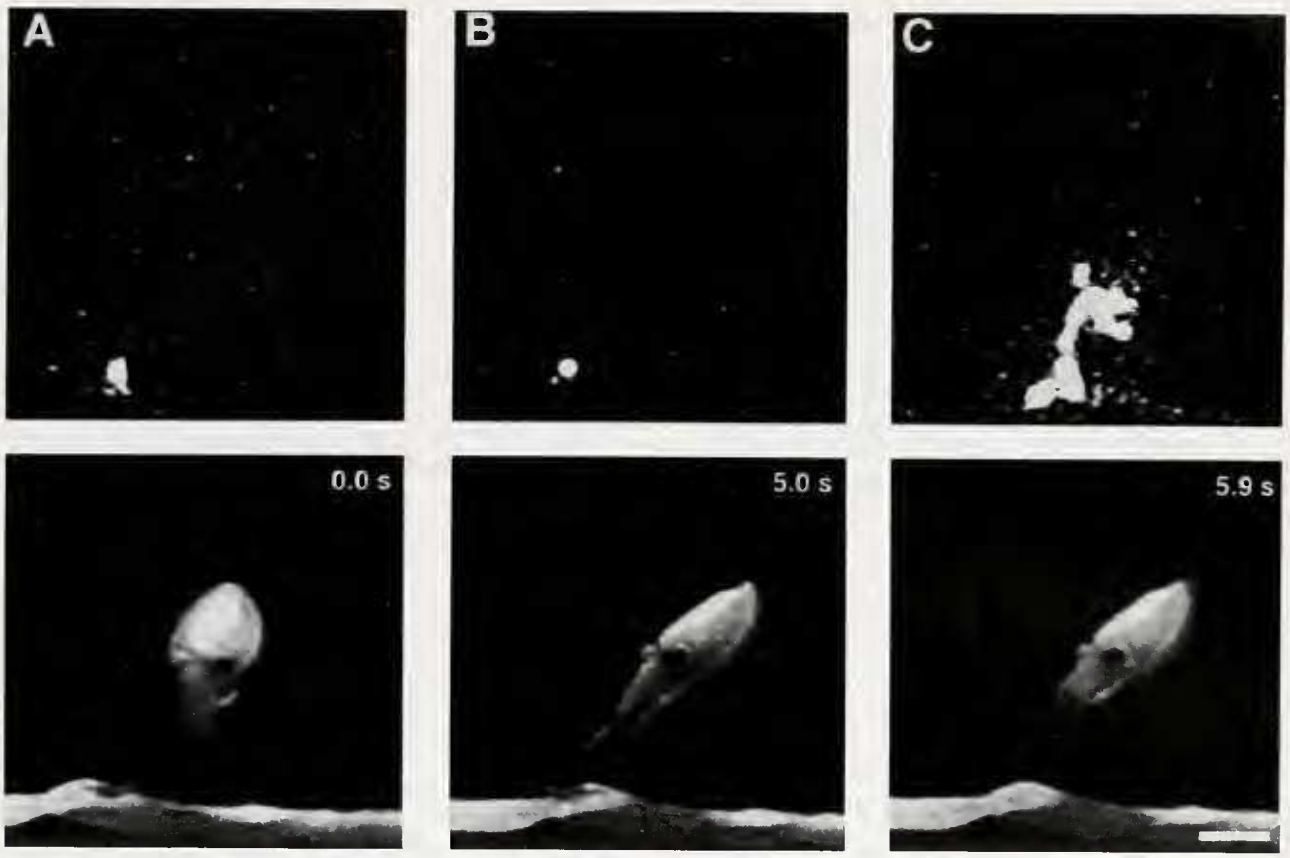

Figure 6. Split-screen video image of *Euprymna scolopes* feeding on ghost shrimp (*Palaemonetes pugio*). Image-intensifying camera, top view. Infrared camera, bottom view. (A) Pre-attack position; (B) Positioning; (C) Seizure. Luminescence is produced by *Pyrocystis fusiformis* stimulated by ghost shrimp movements. Bar scale = 1 cm.

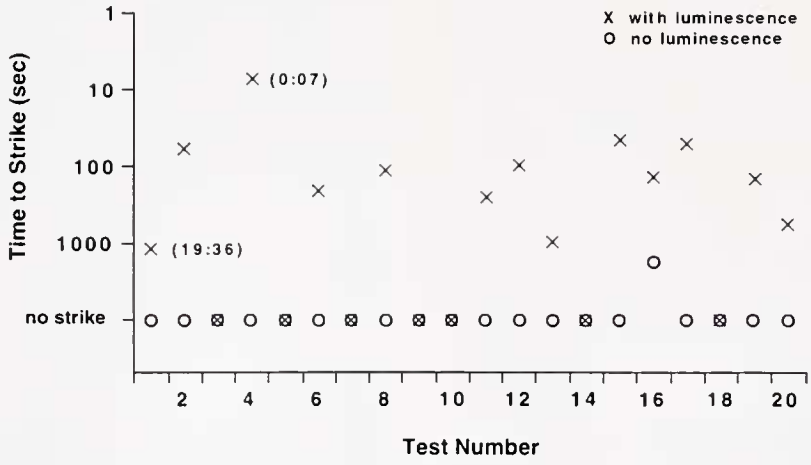

Figure 7. Time required by *Sepia officinalis* to strike mosquito fish (*Gambusia affinis*) in the presence of luminous and nonluminous dinoflagellates (*Pyrocystis fusiformis*).

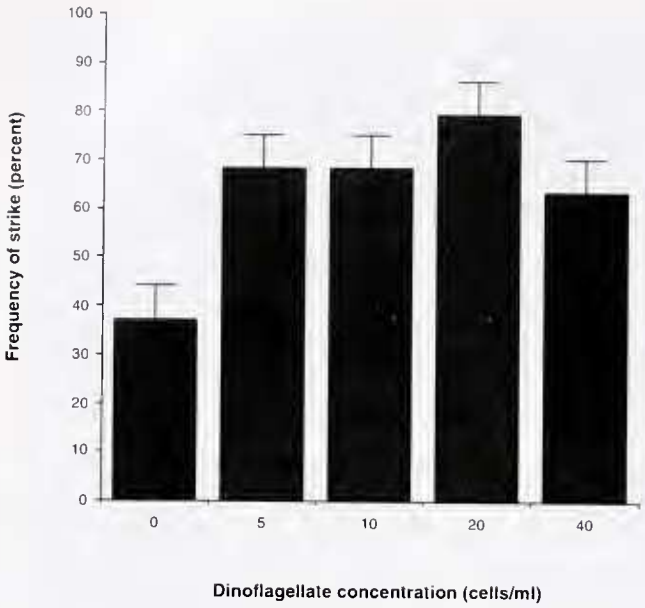

Figure 8. The frequency with which *Euprymna scolopes* attack ghost shrimp (*Palaemonetes pugio*) as a function of concentration of luminescent dinoflagellates (*Pyrocystis fusiformis*). Error bars represent standard errors.

in markedly lower predation. At the same time, the presence of dinoflagellates had no obvious direct detrimental or behavioral effects on prey within the time scale of the experiments.

S. officinalis enters the water column at night to feed. Hovering just off the sand bottom, the cuttlefish either wait for or swim in search of prey. Luminescent dinoflagellates occur naturally in waters off the British coast of France, the Mediterranean, and Great Britain where *S. officinalis* are found. Predation experiments showed that cuttlefish have the ability to use light provided by dinoflagellates to locate prey. Without this light there is little predation success. The higher the dinoflagellate concentration the more prey *S. officinalis* obtained (Fig. 4). We suspect that the ability to regulate bouyancy improves concealment of the cuttlefish from its prey or possible predators by reducing the necessity for locomotor activity.

A difficulty with these experiments was the recovery of luminescence by photophase dinoflagellates in the control tanks (Fig. 2). As bioluminescence competence increased over the 3-hour test, *Sepia* hunted more effectively. Also unexpected was the fact that in total darkness, few prey were attacked. This is contrary to the observations of Budelmann *et al.* (1991), who found that *S. officinalis* uses a lateral line system similar to the mechanoreceptive lateral lines of fish and aquatic amphibians to find about 50% of available prey. In complete darkness, *Sepia* in this experiment consumed significantly less than 50% of available prey (Fig. 4).

Observation of predator/prey interactions with mosquito fish and ISIT/IR video showed that luminescence from dinoflagellates aids *Sepia* to visually locate and strike prey. Prey size and type in these tanks were such that *Sepia* always attacked by discharging its two prehensile tentacles. Video analysis of the predator-prey interactions and correlated bioluminescence clearly showed the eye movements, body orientation, and subsequent strike of individual *S. officinalis* as they followed mosquito fish through luminescent water (Fig. 5). In water populated with scotophase dinoflagellates, 13 out of the 20 *Sepia* successfully struck the prey, and 11 strikes took place in less than 10 min. Without luminescent cells only one strike took place, and this at greater than 29 min. (Fig. 7).

E. scolopes emerges from the sand at night to await prey. Once prey is in an individual's strike zone, the squid orients and strikes—remaining off the bottom for a brief period and then returning to the sand to complete feeding. *E. scolopes* has a slightly different attack mode than *Sepia*. This cephalopod will only strike prey within a defined strike zone and spends little or no time adjusting distance to the prey along the prey axis to ensure seizure (Fig. 6). This, coupled with the highly variable movements of the grass shrimp, may serve to explain the high variance of strike rates. Nonetheless, the frequency with which *E. scolopes* struck was much greater in luminescent water (79%) than in dinoflagellate-free control tanks (37%; Fig. 8). Successful strikes in darkness are unexplainable, but may well involve mechanoreception or near-field acoustic sensitivity. Comparing strikes alone, the rates show no significant differences, indicating no increase or decrease in predation success, due to specific concentration of dinoflagellates. One possible explanation is that the luminescence assisted the squid in locating prey but not necessarily in attack success. Luminescent dinoflagellates occur in measurable quantities on the coast of Hawaii where *E. scolopes* is found.

These experiments, along with those of Mensinger and Case (1992), clearly establish on an experimental basis that predators as widely disparate as fish and cephalopods are able to use the light of dinoflagellates as an effective aid in hunting nonluminescent prey. The work also supports the concept of a more general role for bioluminescence in which detection of bioluminescence, by increasing the sensory domain of nocturnal and deep-sea animals, contributes to their estimation of the carrying capacity of the local environment (Case *et al.*, 1994). Bioluminescent events, typically representing predator/prey interactions, can be seen at several meters distance in clear oceanic waters, and thereby allow animals with good vision to census local populations in a way well beyond the range of sensory modalities other than acoustic.

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